

BIOLOGICAL NOTES ON PARTHENOGENETIC *MACROSIPHUM TANACETI* LINNAEUS(APHIDIDÆ, HOMOPTERA)¹

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The data on which the present paper is based have been collected while I was conducting experiments on *Macrosiphum tanaceti*, in connection with another problem. The work was done at the Bussey Institution during the earlier part of the summer of 1921. A few of the facts brought out in the discussion are somewhat fragmentary, and require more thorough investigation; but, in view of the scarcity of such records of aphid behavior in the literature, they have been introduced here, in the hope that they may help to stimulate further research along these lines.

I. *Ecdysis*. There are no appreciable differences in the behavior of *Macrosiphum tanaceti* during the four successive molts. No attempt, therefore, will be made in the present paper to describe the methods separately for each ecdysis. Preliminary to the process, the nymph ceases to feed for a few minutes, and in the meantime holds with its claws on the surface of the supporting part of the plant. The position of the insect during molting has always been found to be such that the head points toward the ground. The legs are spread far apart, so that the prothoracic pair is directed anterolaterally with reference to the insect's body; the mesothoracic, ectolaterally; and the metathoracic, posterolaterally. The haustellum is held close to the sternum. The subcaudal portion of the abdomen almost touches the surface of the plant. The antennæ are directed posteriorly, and are subparallel to the lateral margin, but diverge at an angle of about thirty degrees above the dorsal surface of the body. A longitudinal mesal rupture then appears at the head, adjoining

¹Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 199.

the base of the clypeus. The insect slowly forces its way through the opening thus made, in the meantime increasing the length of the rent posteriorly along the dorsomedian line of the body, until the caudal margin of the metanotum is reached. The method of formation of the initial rupture has not been observed. Neither has the mechanism of propulsion of the aphid, as it glides by degrees forward, out of the exuviae, been satisfactorily determined. It is, however, evident that the legs are not of assistance until later in the process. In all probability, the force of expansion of the insect's body itself directs the course of the movement through the slit, this opening furnishing the point of least resistance in the tightly fitting exuviae. The head naturally goes out first, being nearest the rupture; and the opening enlarges as the more bulky thorax and abdomen pass out. The pro- and mesothoracic legs soon become disentangled, and it is remarkable how quickly the insect is able to spread them apart and use them to help force the rest of the body out. Apparently, sometime before, or during the earlier part of ecdysis, the chitinous coating of the appendages of the future succeeding instar has a chance to harden. The concluding part of ecdysis, when only the caudal portion of the abdomen and a fraction of the metathoracic tibiae and their tarsi remain in the exuviae, goes on as slowly as the earlier part of the process. The insect never seems to be in a hurry about extricating itself, and, on the whole, the molting of an aphid is an extremely sluggish operation. Finally, the hind legs are set free, but, even then, the insect continues to remain attached with the abdominal cauda enclosed within the ensheathing exuviae. The legs sway up and down and the antennae remain in their posteriorly directed position. Apparently this delay in freeing itself is an important step in the molting process, as it enables the chitinous layer of the body and of the appendages to get dry in the outside air and increase in firmness, until it is safe enough for the insect to turn itself loose. After about five minutes, or so, the fore and middle legs execute a forward crawling motion and the hind legs kick against the exuviae, the aphid ultimately making its escape in this manner. The entire molting process, from the appearance of the initial

rupture to the final escape of the insect, lasts from about twenty to about thirty minutes.² The freshly molted aphid is at once able to walk, but is incapable of resuming feeding until about one-half hour, or more, later.

One other point may be noted here in connection with ecdysis. The layers of the black pigment which in this species give the antennæ, haustellum, wing-pads, legs, cornicles, and abdominal cauda their characteristic piceous color are intimately associated with the chitinous exoskeleton, and are cast off with the exuviae at each molt. They are then formed anew in the succeeding instar. The freshly molted *Macrosiphum tanaceti* is uniformly light green, except the eyes, which are reddish vermillion. The light green color is due to the presence of characteristic green substance in the fat cells and other body tissues, which shows through the semitransparent cuticle. This coloring matter has been the subject of investigation years ago by various workers, notably by Macchiati (1883), who claims to have found chlorophylloid substances in *Siphonophora malvæ* and in *S. rosæ*, and by Przibram (1906, 1909), who has observed that aphids fed on etiolated leaves of onion plants that have been kept in the dark assume the pale yellow color of the latter, suggesting thereby that the green chlorophyll of the plant probably has some relation to the green substance in the aphid tissue. More recently, Glaser (1917) has reported that by chemical tests he has been able to detect the presence of red pigments in *Pterocomma smithiæ* Monell which seem to be localized in the cytoplasm of the fat cells, and which give color reactions suggestive of anthocyanin found in plants.

The characteristic piceous color of the exoskeleton in the regions enumerated above is restored in less than an hour after molting. How this relatively rapid change in color is brought about is difficult to explain. Two possible conditions suggest themselves: (1) After molting, these pigments, with their definitive dark color, are segregated as such by some very active physiological process; or (2) prior to, or during, molting the

²About the same length of time has been observed in *Toxoptera graminum* Rondani by Webster and Phillips (1912).

future dark pigments are deposited in the form of certain achromatic substances and in the succeeding instar assume their characteristic tint upon exposure to light and to other external stimuli.

Janet (1909) has classified in a succinct form the steps involved in ecdysis among insects into four general successive phases. The following quotations from this author are reproduced here for the purpose of comparison and correlation with the foregoing observations and deductions on aphids.

1. "Le décollement de la cuticule ancienne, décollement qui commence généralement dans la région supérieure de la capsule céphalique et se propage vers l'arrière. La cuticule ancienne, décollée, demeure autour du corps sous forme d'une exuvie libre, intacte, et constitue une enveloppe protectrice, momentanément indispensable à cause de la délicatesse de l'épiderme mis à nu."

2. "Accroissement en surface ou transformation du modèle de l'épiderme libéré de sa cuticule."

3. "La formation des premières strates de la cuticule nouvelle, cuticule dont l'apparition rend inutile la protection que fournissait l'ancienne cuticule exuviée."

4. "Le déchirage et le rejet de l'ancienne cuticule."

It appears in the case of the aphids, as well as of other insects, that the above four steps overlap, one into the other. During the detachment of the old cuticle from the insect's body-wall, there undoubtedly occurs simultaneously an increase in surface area of the hypodermal layer. In fact, the stretching effect resulting from the latter cause, together with the steadily augmenting pressure from the developing internal organs, evidently provides the immediate mechanical means for separating the old chitinous from the hypodermal layer. Under the protective cover of the freshly loosened exoskeleton, the new chitinous layer which has been secreted by the hypodermal cells has a chance to develop a firm, although somewhat delicately soft, consistency before the initial rupture appears in the exuvia. In aphids, the hardening of the newly formed exoskeleton occurs mainly during the lengthy process of casting off the old skin.

Summary of Section I. Feeding ceases a few minutes prior to molting. The head of the insect is pointed toward the ground

during the process. The rupture of the chitinous exoskeleton appears first near the base of the clypeus and extends dorsomedially to the posterior margin of the metanotum. The entire molting process, from the formation of the initial rupture until the aphid extricates itself, lasts about thirty minutes. It is able to walk soon after escaping from the exuviae, but is incapable of resuming feeding until about one-half hour, or more, later.

The characteristic piceous color in certain parts of the body is either located in, or intimately associated with, the chitinous exoskeleton, and is cast off at each ecdysis, reappearing, however, in the newly formed integument in less than an hour after molting. The light green color which characterizes the larger portion of the body is due to certain substances in the fat cells showing through the semitransparent cuticle.

The new chitinous layer is deposited sometime before the molt. It has a chance to harden during the lengthy process of casting off the old exuviae.

II. *Locomotion.* The principal and usual method of locomotion, even in alate individuals, is by walking. The wings are used very rarely, and perhaps in connection only with migration from one plant to another when the aphids on a particular host begin to become overcrowded or when the supply of plant sap becomes inadequate. The flight is very feeble, and it is doubtful if the insect can traverse any considerable distance by this means alone.

In walking, the antennæ are directed anteriorly, describing in that position an angle of about forty-five degrees. They continually sway obliquely in alternate turns in an entodorsal and ectoventral direction. The rate of this movement is apparently correlated proportionately with that of the legs; and under ordinary conditions, when the insect is not disturbed, or otherwise excited, the antennæ sway one hundred and twenty times in one minute. This figure has been found to be approximately correct for all instars.

After numerous attempts at following the movements of the legs while the aphid is walking, I have come to the conclusion

that they do not follow any regular schematic sequence. Further, it appears that no two legs move synchronously in the same direction, and that there is no definite rule as to the order in which the legs follow one another. The time intervals between successive steps, irrespective of the sequence of leg movements, appears to be maintained at a uniformly similar rate for a given speed.

Summary of Section II. 1. The principal method of locomotion, even in alate individuals, is walking, the feeble wings being used rarely.

2. The rate of diagonal swaying of the antennæ and the rapidity of walking appear to be correlated, the movement of the former being in direct proportion to that of the latter.

3. The movement of the legs do not follow any regular schematic sequence, although the time intervals between successive steps appear to be uniformly maintained in a given speed. No two legs move synchronously.

III. *Feeding Habits.* *Macrosiphum tanaceti* has been known to occur only on *Tanacetum vulgare* Linnaeus. This species of aphid apparently has no secondary host plant.

No attempt will be made in the present work to describe the mechanical and physiological relation of the mouth-parts to the plant tissue during the process of feeding. Considerable work has been done in connection with this problem in comparatively recent years, notably by Büsgen (1891), and by Zweigelt; the latter author has been working on this and related subjects during the past decade. Zweigelt (1915) suggests the following three possible means by which suction of plant sap is accomplished in aphids.

“1. Eine bestimmte Zelle wird angestochen und ohne Verletzung der äusseren Hautschicht des Protoplasten ausgesaugt; 2. die Aussaugung bestimmter Zellen erfolgt während deren vollständiger Durchbohrung; 3. die Aussaugung geht zufolge einer dem Speichel innewohnenden starken osmotischen Saugkraft bei interzellularem Stichverlauf ohne mechanische Verletzung der Zellen vor sich.”

Macrosiphum tanaceti feeds on the growing regions of the stem, on which different instars of this species are found in large numbers from early spring until late in the fall in Boston and vicinity. The more succulent portions of the petioles are also feeding places for the later nymphal instars and the adults, although they are found here only occasionally. While the aphid is feeding, its head points toward the ground, the antennæ are directed lateroposteriorly with reference to the body, and the legs are spread apart. The haustellum is at right angles with the body or inclined somewhat anteriorly. The labium, which serves as the sheath for the rest of the mouth-parts, except the labrum, remains straight. No posterior bending is observed at the point of junction of any two labial segments, which is a characteristic feeding habit of the members of a closely allied order, the Heteroptera. The latter group resorts to this contrivance in order to enable the setæ to penetrate deeper into the plant tissues. In *Macrosiphum tanaceti* the tips of the setæ apparently do not go far beneath the epidermis of the plant, perhaps reaching only a small portion of the cortical layer. This supposition is based on the fact that in all the specimens examined while in the act of feeding it was found that the setæ protrude less than a millimeter beyond the distal end of the labial sheath.

The position assumed by the insect while feeding is interesting. It is not easy to see why the insect should prefer to remain in that seemingly uncomfortable posture in which the abdomen is situated uppermost. The following experiments were conducted in order to find out the possible explanation for this peculiar habit:

Growing tips of *Tanacetum vulgare*, with numerous tansy aphids in different instars feeding on them, were carefully bent down without injuring the plants and were made to remain in this position by fastening them with strings. In this way, the aphids, without being disturbed, are reversed in their position, now with the head uppermost. These experiments were performed in the morning when it was still cool, at noon, when the sun was very bright and the temperature was about 32° C. (90° F.) and in the evening when it was almost dark. The results in all

cases have been found to be identical: The aphids sooner or later return to their former position, that is, with the abdomen uppermost and the head directed toward the ground. The degree of ability to orient itself in this manner apparently differs with the age and morphological characters of the individual. The alate adults turn around almost instantly after their former position is reversed. The nymphs in the first instar are the slowest to respond to the treatment. The later nymphal instars of the future alate and apterous individuals and the apterous adults do not react at once, as in the case of the winged adults, although the response takes place much more quickly than in the first-instar nymphs.

The following interpretations are offered for the foregoing behavior: the tansy aphid, like the parthenogenetic forms of the other species of this family, feeds practically all the time. It is interrupted in this activity only when it changes its feeding location, after the supply of food material in a given part of the plant becomes temporarily used up. In a healthy plant, where there is an abundance of succulent tissue at the growing region, this change in location takes but a short time. The feeding operations, of course, require that the aphid remain stationary in one position during the process, and, consequently, it has to stand still almost all the time. Now, under these conditions, prolonged exposure to the direct rays of the sun, especially at midday, when they are very intense, is undoubtedly uncomfortable, if not ruinous, to the eyes of the aphids. The tansy plants generally grow in unsheltered places and the growing tips on which the aphids feed are fully exposed to the sun. The habitual position of *Macrosiphum tanacetii* is probably an adaptation to that environmental condition. By locating itself on the plant in such a way that the aphid's head is directed downward, the rays of bright sunlight from above do not strike the eyes directly. With this view in mind, however, it is difficult to find an explanation for the maintenance of the same behavior by the insect in the morning, when the rays of light are not so intense, and in the evening when it is almost dark. One probability is that the heliophobic reaction of the aphid has brought about secondary

effects which cause the insect to assume this position irrespective of the immediate presence of the causative stimulus.

One other explanation may be offered here: The aphid possibly assumes this position for mechanical advantage, in the way of bringing about optimum efficiency in the functions of the sucking mouth-parts, and of minimizing the strain on the muscles of the legs and other parts of the body which is occasioned by the insect's having to remain in one position for considerable lengths of time while feeding.

The fact that the aphids turn around and resume feeding in the reverse direction with respect to the plant when the tips of the tansy on which they are situated are bent indicates that this behavior of *Macrosiphum* has not been brought about as an adaptation to any peculiarity in the structure of the host.

The characteristic feeding position of *Macrosiphum tanacetii* has also been observed by me in other species of *Macrosiphum*. It is interesting to note that the aphids of other genera which I have studied³ do not seem to exhibit this peculiarity. They almost all indifferently assume any position while feeding. It may be mentioned, as a possible explanation of this difference in behavior, that these other aphids generally feed on the nether surface of broad leaves, or are otherwise protected from the direct rays of the sun. Thus the main stimulus which, as I have suggested above, is probably responsible for the characteristic position of the *Macrosiphum* species is suppressed in the case of the other aphids.

Summary of Section III. 1. *Macrosiphum tanacetii* appears to be confined to a single host plant, *Tanacetum vulgare*. From early in the spring until late in the fall in Boston and vicinity, this aphid in different instars is found feeding on the more succulent portions of the plant, principally on the growing regions of the stem.

2. The head of the insect is directed toward the ground

³Anoecia, Lachnus, Longistigma, Drepanaphis, Drepanosiphum, Myzus, Eriosoma, unidentified aphids on *Berberis vulgaris* Linn., *Celastrus scandens* Linn., *Lythrum salicaria* Linn., *Sherpherdia (Elaeagnus) argentea* Nutt., and *Viburnum* sp., and others.

during feeding, as in ecdysis, which has been previously described. One or both of the following explanations may account for this peculiar behavior: (1) In order to avoid the rays of the sun from streaming directly into the eyes. (2) For mechanical advantage, the feeding apparatus perhaps attaining its maximum efficiency or the strain on the muscles being probably minimized when the aphid assumes this position. The second explanation is purely speculative. This characteristic position is evidently not an adaptation to any peculiarity in the structure of the host.

3. The setæ of this aphid apparently do not penetrate very deeply into the plant tissue.

IV. "Death-Feigning." The habit of dropping to the ground when disturbed and remaining motionless for a time is a very peculiar characteristic which is exhibited by many species of *Macrosiphum*.⁴ *M. tanacetii* responds readily in this manner and on reaching the surface of the ground, the insect behaves in either of the following two ways, depending on its position after it drops: (1) If it lands on its ventral side, it simply stands on its legs and remains motionless in this attitude. The antennæ are directed posteriorly. (2) If it lands on any part of the body other than the ventral side, the legs are folded so that the tibiæ are also directed posteriorly and the insect remains perfectly quiet.

The nymphs of the first instar do not seem to have the ability of "death-feigning" to any marked degree. They are practically the only ones that remain on the plant, after the latter is jarred and individuals of the second and later instars drop to the ground. The adult individuals always regain their standing position very quickly and remain in this position, no matter which portion of the body touches the ground first. The wings remain folded and the insect does not seem to use them as it falls.

The biological significance of this peculiar behavior has been the subject of discussion and speculation by various workers who

⁴In my own work, I have not come across a single species of *Macrosiphum* which does not exhibit "death-feigning." However, Dr. A. C. Baker, of the Bureau of Entomology, U. S. Department of Agriculture, in a letter dated at Washington, D. C., January 18, 1922, informs me that there are some *Macrosiphum* species which do not possess this habit. He further mentions the interesting fact that "death-feigning" is not confined to *Macrosiphum*, for this peculiarity is also met with in the Callipterina.

have observed it in other groups of insects, notably by Fabre on *Scarites gigas* Fabricius (Coleoptera); by Holmes on *Ranatra* sp. (Heteroptera); and by Rabaud and by Bohn on several orders (Bouvier, 1919, pp. 79-89). In *Macrosiphum* the habit of dropping to the ground and remaining motionless for a time is evidently a means of eluding a pursuing enemy.

Summary of Section IV. Many species of *Macrosiphum* possess the habit of "death-feigning" when disturbed.

2. The habit is exhibited by *Macrosiphum tanacetii* in all of its stages, except in the first instar.

V. *Parturition.* At birth, the caudal portion of the nymph appears first at the vaginal slit. The antennæ are directed posteriorly and closely appressed to the body walls. The legs and cornicles are also in the same condition, the appendages thus following the general contour of the body. The tarsi of the metathoracic legs are in intimate contact with each other, forming at the caudal portion of the abdomen a conspicuous acutely subconical projection. The color of the nymph at birth resembles that of the freshly molted nymph or adult. The body and appendages are uniformly light apple-green and glossy, and the eyes are reddish vermillion. The enveloping membrane covering the young at birth, which has been described by Webster and Phillips (1912) in *Toxoptera graminum* Rondani, by Baker (1915) in *Eriosoma lanigerum* Hausman, and by other authors in other species of aphids, has also been observed by me in *Macrosiphum tanacetii*. The results of the present work agree with Baker's account in that the envelope ruptures while the nymph is partially extruded from the vaginal slit of the mother. The nature of this membrane is still in question; although, from my observations on *M. tanacetii*, I am led to believe that it probably arises from the follicular epithelium, which persists to this stage without degenerating. A more detailed discussion of this subject will be given in a later paper on aphid embryology which I am publishing. If my observations, therefore, are correct, this envelope is not a homologue of the vitelline membrane of the eggs of amphigonous aphids, as Webster and Phillips have

claimed, since the latter membrane arises as a secretion of the egg-periplasm, and has no direct relation to the follicular epithelium.

The extrusion of the nymph from the vagina, from the time the caudal portion of the abdomen of the former begins to protrude until the entire body is exposed, takes about five or ten minutes. The insect remains in the condition described above, attached by the anterior margin of the head and the bases of the antennæ to the external opening of the mother's vagina for about ten or fifteen minutes. At the end of this time, the young insect has dried its skin well enough to set the appendages free from their attachment to the body. A waving motion of the antennæ and of the legs then ensue; but the nymph does not seem to struggle to make its final escape. After about five more minutes, the chitinous exoskeleton has probably hardened sufficiently, and the mother then executes two or three sudden peristaltic movements of the abdomen, which set the young nymph free. The newly born aphid usually remains in close proximity to the place where it is deposited by the mother. In about fifteen or twenty minutes after birth the nymph begins feeding, and by this time also the characteristic colors of the body and appendages become evident.

The position of the mother during parturition is the same as that described in connection with her feeding habits. The abdomen is situated uppermost and the head directed toward the ground. In fact, parturition goes on simultaneously with feeding, apparently without in the least interfering with the latter process.

Summary of Section V. 1. At birth, the young makes its appearance with the caudal portion of the body first.

2. After extrusion from the vagina, the nymph remains attached by the anterior margin of its head to the vaginal slit of the mother until the exoskeleton of the young hardens. The process requires about ten to fifteen minutes, when the nymph finally becomes separated from the mother.

3. At birth, the nymph is covered with a membraneous envelope which usually ruptures when the former is partially extruded through the vaginal slit. The nature of this envelope is still in question. I infer from my own observations on *Macrosiphum tenaceti* that the membrane arises from the egg-follicle, which apparently does not degenerate.

4. The nymph begins to feed in about fifteen to twenty minutes after birth.

5. The position of the mother during parturition is the same as in feeding. Parturition apparently does not interfere with the latter process.

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